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Accounting for connectivity and spatial correlation in the optimal placement of wildlife habitat

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Abstract

This paper investigates optimization approaches to simultaneously modelling habitat fragmentation and spatial correlation between patch populations. The problem is formulated with habitat connectivity affecting population means and variances, with spatial correlations accounted for in covariance calculations. Population with a pre-specified confidence level is then maximized in nonlinear programs that define habitat patches as circles (fixed shape) or rectangles (variable shape). The ideas and model formulations are demonstrated in a case example with a maximum of four habitat patches. Spatial layout of habitat is strongly sensitive to species dispersal characteristics and the spatial correlation structure resulting from different environmental disturbance agents.

Keywords: Landscape structure; Nonlinear programming; Patchy environments; Spatial patterns

1. Introduction

Increasing human populations are resulting in greater resource development pressures and land use intensification. One outcome is a reduction and insularization of natural habitats – a pattern often discussed under the rubric of landscape fragmentation. Animal species associated with natural habitats will thus exhibit a patchy distribution over a mosaic of suitable and unsuitable habitat (Gilpin, 1987) with population dynamics over the landscape being affected by the spatial pattern of fragmentation (Hanski, 1991).

It is commonly predicted that wildlife population establishment and persistence is lower in fragmented habitats than in well-connected habitats resulting in more susceptibility to extinction (Diamond, 1976; Fahrig and Merriam, 1985; Burkey, 1989; Tilman et al., 1994). In addition to this demographic extinction pressure (sensu Shaffer, 1981), there is concern that wildlife populations are vulnerable to environmental stresses (e.g., fire, extreme weather events, and disease) that have varying magnitudes of spatial covariance (Simberloff and Abele, 1976; den Boer, 1981; Goodman, 1987; Quinn and Hastings, 1987). By spreading the risk of environmental stress among subdivided populations, persistence time may actually be longer in fragmented landscapes (Fahrig and Paloheimo, 1988).

The need for connectivity to minimize demographic extinction pressures suggests that a desir-

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able spatial layout of habitat fragments would involve highly "clumped" patches, whereas the possibility of spatially-correlated ruinous events suggests that some degree of habitat spreading may be advantageous. This paper provides a statistically-based formulation for mathematically capturing both of these considerations, and explores some mathematical (nonlinear) programming approaches for finding an optimal balance in this ecological trade-off.

2. Theory

Because resource managers are confronted with competing uses for a finite land base, we assume that only a fraction of that finite land base will be retained as habitat. We then assume that the problem is to arrange the remaining habitat in a spatially optimal manner that meets specified population objectives for a certain wildlife species. We also assume that habitat placement is semipermanent, so there is no scheduling element to consider.

2.1. Connectivity

The ecological literature (for review see, Wilson and Willis, 1975; Diamond, 1975; Simberloff, 1988) has recommended that a single large area is better than several smaller areas, and if subdivision cannot be avoided, habitats clustered to minimize distances between patches are preferred to those arranged linearly. Likewise, a circle of remnant habitat is better than an oblong shape (Game, 1980). These recommendations are based on a notion that wildlife disperse in a directionless or random fashion. There would thus be some probability that a given habitat area around any other habitat area would be "connected", and this probability would diminish as the distance increases between the two habitat areas. With many habitat areas, the probability of a given area being connected would be a function of the number of other habitat areas nearby and the distances to them. We assume that the probability of each area being connected to a group of areas is the joint probability that the area is connected to *any* (not all) of the areas in the group. We also assume independence between the individual connectivity probabilities. Thus, the joint probability (PR_i) of each patch i being connected would be:

$$PR_i = 1 - \left[\prod_{j=1}^{M} (1 - pr_{ij}) \right] \quad \forall i \tag{1}$$

where pr_{ij} is the probability that patch i is connected to patch j (pr_{ii} assumed to be 0). Presumably, pr_{ij} would be smaller, the farther patch j is from patch i. Eq. 1 simply calculates the joint probability that patch i is not connected to any of the $j = 1, \cdots, M$ ($j \neq i$) patches, and then calculates PR_i as the converse of that joint probability. At some distance, the probability of two habitat areas being connected would be effectively zero. Thus, when an area is retained as habitat, it has a certain probability of being connected, which is determined by the number and location of other habitat areas, and it also contributes to the probability of other areas being connected in an equivalent manner. We discuss specific functional relationships between pr_{ij} and inter-patch distance in the case example.

If we assume that habitat is only used to the degree that it is connected, it would be reasonable to define the expected population in the ith patch, $E(P_i)$, as:

$$E(P_i) = PR_i a_i S_i$$

and the expected value of the total population $E(P)$ as:

$$E(P) = \sum_{i=1}^{M} PR_i a_i S_i \tag{2}$$

where: a_i = the expected density of individuals in perfectly-connected habitat in the ith patch; S_i = the size of the ith patch.

Eq. 2 calculates $E(P_i)$ for each patch as the expected population of a perfectly-connected patch ($a_i S_i$) times the probability that it is connected (PR_i), and then sums across patches to obtain $E(P)$. We will initially assume that the a_i are fixed constants, but will also investigate alternative formulations that will account for the influence of patch size and shape.

2.2. Spatial correlation

A number of investigators have noted that populations across different patches of habitat are spatially correlated (Gilpin, 1987; Fahrig and Merriam, 1994). Varying degrees of synchrony in population dynamics occur because distance often determines the commonality of random influences (e.g., weather, fire) on populations, including influences that are directly affected by population connectivity (e.g., disease, genetic variation). Applying the standard definition of covariance to any two patch populations implies:

$$\sigma_{ij}^2 = \rho_{ij}\sigma_i\sigma_j$$

where: σ_{ij}^2 = the covariance between the population in patch i and the population in patch j. ρ_{ij} = the correlation between the population in patch i and the population in patch j. σ_i, σ_j = the standard deviations of the populations in patches i and j, respectively.

Then, the total population variance, $\mathrm{V}(P)$, will be:

$$\mathrm{V}(P) = \sum_{i=1}^{M}\sum_{j=1}^{M}\rho_{ij}\sigma_i\sigma_j \tag{3}$$

If the ρ_{ij} are negatively related to the distance between patch i and patch j, then spreading of the patches could be desirable because it reduces the pairwise correlations. This reduces the variance of the total population, thus reducing the probability of a catastrophically-low population, all other things (especially $\mathrm{E}(P)$) being equal.

There is also typically some relationship between each σ_i and $\mathrm{E}(P_i)$. For convenience (only) we will assume a fixed coefficient of variation for the population of each patch implying:

$$\sigma_i = \psi\mathrm{E}(P_i) \quad \forall i$$

where ψ is a fixed constant. Thus, by Eq. 2, Eq. 3 can be written as:

$$\mathrm{V}(P) = \sum_{i=1}^{M}\sum_{j=1}^{M}\rho_{ij}(\psi\mathrm{PR}_i a_i S_i)(\psi\mathrm{PR}_j a_j S_j) \tag{4}$$

Specific relationships between the ρ_{ij} and interpatch distance are discussed in the case example.

2.3. Chance maximization

Both connectivity and spatially correlated environmental disturbances can be captured with a mathematical statement of a given confidence level for total population:

$$B = \mathrm{E}(P) + \delta\mathrm{V}(P)^{1/2} \tag{5}$$

where δ = the "z-value" or standard deviate for the given confidence level; B = the population associated with the given confidence level.

Thus, for example, we can calculate the population that we are 80% ($\delta = -0.84$) confident in as (using Eqs. 2 and 4):

$$B = \sum_{i=1}^{M}\mathrm{PR}_i a_i S_i - 0.84\left[\sum_{i=1}^{M}\sum_{j=1}^{M}\rho_{ij}(\psi\mathrm{PR}_i a_i S_i) \times (\psi\mathrm{PR}_j a_j S_j)\right]^{1/2} \tag{6}$$

It is clear that the size and location of the habitat patches affect B through both the mean and the variance of P in Eq. 5. We assert that it would be desirable to maximize B with a selected δ subject to resource limitations (it would also be reasonable to fix B and minimize δ). The remainder of this paper will investigate mathematical programming approaches to this problem, which tie the PR_i and ρ_{ij} variables to specific patch layouts and then optimize those layouts to maximize B. This mathematical programming problem should be distinguished from those typically addressed with simulation modelling which can analyze population impacts of a given spatial layout (see Kareiva, 1990) but does not find an optimal layout, per se.

3. Optimization

We will link the ρ and PR variables to habitat patch layouts using geometric shapes: first circles and then rectangles. Problems with circular patches have a simpler formulation, but the rectangular patches afford more flexibility in terms of patch shape (square vs. long and narrow, etc.). Choice variables will be established to define location and size (and shape in the case of the rectangles) of habitat patches from which distances can be calculated in the mathematical programs. It is necessary to pre-specify the maximum number of habitat patches (M).

3.1. Circles

We located the circular habitat patches with their centroids in a system of east/west–north/south (x–y) coordinates. The size of each circle was then characterized by the radius, and the distance between any two circles was simply the distance between their centroids less the sum of their radii. A mathematical (nonlinear) program to maximize B with circular patches can thus be formulated as follows:

Maximize:

$$B = \mathrm{E}(P) + \delta \mathrm{V}(P)^{1/2}$$

Subject to:

$$\mathrm{E}(P) = \sum_{i=1}^{M} \mathrm{PR}_i a_i S_i$$

$$\mathrm{V}(P) = \sum_{i=1}^{M} \rho_{ii} (\psi \mathrm{PR}_i a_i S_i)^2 + \sum_{i=1}^{M} \sum_{j>i} 2\rho_{ij} (\psi \mathrm{PR}_i a_i S_i)(\psi \mathrm{PR}_j a_j S_j)$$

$$\mathrm{PR}_i = 1 - \left[\prod_{j=1}^{M} (1 - \mathrm{pr}_{ij}) \right] \quad \forall i \tag{7}$$

$$\mathrm{pr}_{ij} = f(D_{ij}) \quad \forall i, \quad j > i \tag{8}$$

$$\rho_{ij} = g(D_{ij}) \quad \forall i, \quad j > i \tag{9}$$

$$\sum_{i=1}^{M} S_i \le \overline{L} \tag{10}$$

$$x_i \ge r_i \quad \forall i \tag{11}$$

$$y_i \ge r_i \quad \forall i \tag{12}$$

$$x_i + r_i \le \overline{X} \quad \forall i \tag{13}$$

$$y_i + r_i \le \overline{Y} \quad \forall i \tag{14}$$

$$S_i = \pi r_i^2 \quad \forall i \tag{15}$$

$$D_{ij} = \left[(x_i - x_j)^2 + (y_i - y_j)^2 \right]^{1/2} - (r_i + r_j) \quad \forall i, j > i \tag{16}$$

$$D_{ij} \ge 0 \quad \forall i, \quad j > i \tag{17}$$

$$r_i \ge \overline{R} \quad \forall i \tag{18}$$

where: f and g = generic functions – possible specific functions will be discussed below; D_{ij} = the distance between circle i and circle j; $\overline{L}$ = the amount of habitat area that can be retained; $\overline{X}$ = the east–west dimension of the problem space; $\overline{Y}$ = the north–south dimension of the problem space; x_i = the x-coordinate of the center of the ith circular habitat patch; y_i = the y-coordinate of the center of the ith circular habitat patch; r_i = the radius of the ith circular habitat patch; and all other variables are as previously defined.

The optimization process will thus choose levels of x_i, y_i, and r_i that size and locate the habitat circles so as to maximize B. Eq. 7 merely repeats Eq. 1 and calculates the joint probability of connectivity for each patch i. Eq. 8 calculates the pairwise probability of connectivity for each i and j pair as a function of distance. Similarly, Eq. 9 calculates the correlation for each i and j pair as a function of distance. Eq. 10 limits the total amount of retained habitat to $\overline{L}$. Eqs. 11–14 keep the circles of habitat within the problem space, which is assumed to be rectangular with dimensions $\overline{Y}$ by $\overline{X}$. Eq. 15 calculates the area of each circle, and Eq. 16 calculates the distance between each pair of circles. Eq. 17 prevents the circles from overlapping. Eq. 18 sets the minimum radius for each habitat circle. If it is desired to allow radii (and thus circle areas) to go to zero, the contribution to population variance will automatically be removed in Eq. 6 (see also Eq. 3). D_{ij} would have to be multiplied by $S_i S_j/(S_i S_j + \epsilon)$ in Eq. 8, where ϵ is an arbitrarily small constant, in order to remove any contribution of a zero-area circle to connectivity. This would allow selection of the number of habitat patches, within the maximum allowed number, M. If the number of patches is to be pre-specified (again, as M), then $\bar{R}$ should be set at the minimum size that functions as a patch in the model in terms of carrying capacity, connectivity, and covariance.

In the formulations up to this point, we have treated the a_i as a fixed constant. For many species, the density of population is not a simple linear function of habitat area. Often, edge habitats – habitats near the boundary of the patch – have either unsuitable microclimates or harbor predators and competitors that can reduce the population. Consequently, as the proportion of edge habitat increases relative to patch area, the expected value of the population should decline. To account for this phenomenon, we defined a buffer distance b from the habitat patch edge, inside of which edge-associated population decimation factors fail to affect population density. We could then penalize a_i as follows (to define α_i):

$$\alpha_i = a_i(S_\mathrm{T} - S_b)^\gamma \quad 0 \le \gamma \le 1$$

where S_T is total patch area, S_b is the area of the buffer, and γ reflects the degree to which species can survive and reproduce in the edge habitats. If the edge habitats are totally unsuitable, then $\gamma = 1$ and the effective habitat area (SS_i) could be calculated as:

$$\mathrm{SS}_i = \pi(r_i - b)^2 \quad \forall i$$

and SS_i would replace S_i in Eq. 6, but not Eq. 10 which constrains the total habitat area and Eq. 15 which defines the S_i. The a_i would thus still be fixed, because the nonlinearity is accounted for in calculating SS_i. Because the shape of the circles is invariant, this only penalizes small size patches in terms of habitability. We next turn to a formulation that utilizes rectangles, so that shape of the patches is more variable.

3.2. Rectangles

Our approach with rectangles of habitat is similar, but Eqs. 11–18 need to be replaced to account for the different geometry. For convenience, we located the ith rectangle by the x–y coordinates (x_i^0 and y_i^0) of its southwest (lower-left-hand) corner. The size and shape of each habitat rectangle was then determined by two choice variables (x_i^* and y_i^*) specifying its x dimension and its y dimension.

Calculating the distance between rectangles is more complicated than with circles, because of the variable shape. Let us define the x and y vectors between the closest points of two rectangles (i and j) as Δx and Δy. Then note that the distance between i and j is always:

$$D_{ij} = \sqrt{\Delta x^2 + \Delta y^2}$$

which is Δx if $\Delta y = 0$, Δy if $\Delta x = 0$, and the hypotenuse of the triangle formed by Δx and Δy if $\Delta x > 0$, $\Delta y > 0$.

Now, looking first at the x vector, there are three cases to consider:

(a) rectangle i is completely to the left of rectangle j, so $\Delta x = x_j^0 - (x_i^0 + x_i^*)$,
(b) rectangle i is completely to the right of rectangle j, so $\Delta x = x_i^0 - (x_j^0 + x_j^*)$, and
(c) rectangles i and j are at least partially above/below each other, so $\Delta x = 0$.

Note that in case (a) $x_i^0 - (x_j^0 + x_j^*)$ is negative and that in case (b) $x_j^0 - (x_i^0 + x_i^*)$ is negative.

Similarly, looking at the y vector, there are three cases to consider:

(d) rectangle i is completely below rectangle j, so $\Delta y = y_j^0 - (y_i^0 + y_i^*)$,
(e) rectangle i is completely above rectangle j, so $\Delta y = y_i^0 - (y_j^0 + y_j^*)$, and
(f) rectangles i and j are at least partially left/right of each other, so $\Delta y = 0$.

Note that in case (d) $y_i^0 - (y_j^0 + y_j^*)$ is negative and that in case (e) $y_j^0 - (y_i^0 + y_i^*)$ is negative.

It will be useful to define the following instrumental variables:

$$\mathrm{DX}_{ij}^1 = 0.5\sqrt{\left(x_j^0 - x_i^0 - x_i^*\right)^2} + 0.5\left(x_j^0 - x_i^0 - x_i^*\right)$$

$$\mathrm{DX}_{ij}^2 = 0.5\sqrt{\left(x_i^0 - x_j^0 - x_j^*\right)^2} + 0.5\left(x_i^0 - x_j^0 - x_j^*\right)$$

$$\mathrm{DY}_{ij}^1 = 0.5\sqrt{\left(y_j^0 - y_i^0 - y_i^*\right)^2} + 0.5\left(y_j^0 - y_i^0 - y_i^*\right)$$

$$\mathrm{DY}_{ij}^2 = 0.5\sqrt{\left(y_i^0 - y_j^0 - y_j^*\right)^2} + 0.5\left(y_i^0 - y_j^0 - y_j^*\right)$$

For example, DX_{ij}^1 is zero if $x_j^0 - x_i^0 - x_i^*$ is negative, but is $x_j^0 - x_i^0 - x_i^*$ otherwise. Case (a) implies $DX^1_{ij} > 0$ and $DX^2_{ij} = 0$; case (b) implies $DX^1_{ij} = 0$ and $DX^2_{ij} > 0$; and, case (c) implies $DX^1_{ij} = 0$ and $DX^2_{ij} = 0$. With these instrumental variables, it is then possible to calculate the distance between rectangle i and rectangle j as:

$$D_{ij} = \left[\left(DX^1_{ij}\right)^2 + \left(DX^2_{ij}\right)^2 + \left(DY^1_{ij}\right)^2 + \left(DY^2_{ij}\right)^2\right]^{1/2} \tag{20}$$

with the restriction that:

$$DX^1_{ij} + DX^2_{ij} + DY^1_{ij} + DY^2_{ij} \geq \mu$$

where μ is an arbitrarily small (but nonzero) positive constant, to prevent the two rectangles from overlapping. The constant μ must be selected to exceed the precision of the instrumental variable calculations, as it works by forcing at least one instrumental variable to be > 0. Eq. 20 is simply a re-statement of Eq. 19, using the instrumental variables to "zero-out" the incorrect calculations of Δx and Δy so that Eq. 20 is general to all combinations of cases (a)-(b)-(c) with cases (d)-(e)-(f).

A mathematical (nonlinear) program to maximize B with rectangular patches can thus be formulated by replacing Eqs. 11–18 in the circle formulation with:

$$x_i^0 \geq 0 \quad \forall i \tag{21}$$

$$y_i^0 \geq 0 \quad \forall i \tag{22}$$

$$x_i^0 + x_i^* \leq \overline{X} \quad \forall i \tag{23}$$

$$y_i^0 + y_i^* \leq \overline{Y} \quad \forall i \tag{24}$$

$$S_i = x_i^* \cdot y_i^* \quad \forall i \tag{25}$$

$$D_{ij} = \left[\left(DX^1_{ij}\right)^2 + \left(DX^2_{ij}\right)^2 + \left(DY^1_{ij}\right)^2 + \left(DY^2_{ij}\right)^2\right]^{1/2} \quad \forall i, \quad j > i \tag{26}$$

$$DX^1_{ij} + DX^2_{ij} + DY^1_{ij} + DY^2_{ij} \geq \mu \quad \forall i, \quad j > i \tag{27}$$

$$x_i^* \geq \overline{Q} \quad \forall i \tag{28}$$

$$y_i^* \geq \overline{Q} \quad \forall i \tag{29}$$

Eqs. 21–24 keep the rectangles of habitat within the problem space, as previously defined. Eq. 25 calculates the area of each habitat rectangle. Eq. 26 calculates the distances between rectangles, and Eq. 27 prevents overlaps, as just described. $\overline{Q}$ is the minimum size of each dimension of each rectangle of habitat. The same adjustment to Eq. 8 (as in the circle formulation) would be necessary if it is desired to set $\overline{Q} = 0$. All other variables are as previously defined.

In order to account for unusable buffer areas near edges, as discussed for the circle formulation (and again assuming that the buffer areas are completely unsuitable as habitat), we could define:

$$SS_i = (X_i^* - b)(Y^* - b) \quad \forall i$$

and replace S_i with SS_i in Eq. 6. This penalizes long, narrow shapes as well as small sizes of rectangular habitat patches. It should be noted that if only shape is to be penalized, this would be possible by replacing a_i with α_i defined in a manner such as:

$$\alpha_i = a_i\left(\frac{4\sqrt{S_i}}{2x_i^* + 2y_i^*}\right)^{\lambda}$$

(see Austin, 1984) which would penalize the a_i for shapes as they deviate from squares, at a rate determined by λ $(0 \leq \lambda \leq 1)$.

4. Case example

4.1. Problem definition

In order to construct a case example, we scaled the spatial optimization problem to the ecology of a hypothetical species that defends a 1-ha territory and each territory represents a single breeding pair. These life history attributes are not entirely arbitrary but are characteristic of an avian, habitat-interior specialist (see Temple and Cary, 1988). We defined patch connectivity as the probability of individuals successfully immigrating from patch i to patch j. Patch connectivity is thus a function of distance between patches (measured as the minimum edge-to-edge distance), the dispersal capability of the species, and the harshness of the inter-patch environment. A continuous function for pr_{ij} that declines monotonically with distance and approaches zero asymptotically is given by:

$$\text{pr}_{ij} = \text{pr}^0 - \text{pr}^0(1 - \theta^{D_{ij}})^{\beta} \quad (30)$$

where β reflects species dispersal capability and sets a threshold distance beyond which the probability of successfully colonizing a patch declines relatively rapidly, and θ reflects the harshness of the inter-patch environment which affects the rate of decline. The parameter pr^0 indicates the probability of connectivity when $D_{ij} = 0$.

The formulations also require a function that relates patch correlation ρ_{ij} to distance (D_{ij}). Clearly, the correlation between patch populations increases as the distance between patches declines. However, the correlation among patches is also affected by the type of environmental disturbance agents that affect long-term population persistence. For example, population dynamics in fragmented habitats would have an inherently different ρ_{ij} structure if the disturbance agent is a disease transmitted by contact among individuals as opposed to a disturbance agent unaffected by patch population interactions (e.g., severe drought). We represent ρ_{ij} as a function of distance between patches as:

$$\rho_{ij} = \rho^0 - \rho^0(1 - \omega^{D_{ij}})^{\tau}$$

where τ reflects a threshold distance beyond which the correlation between patches declines relatively rapidly, and ω reflects the rate at which the spatial covariance among patches decreases with distance. Both τ and ω are disturbance-specific. The parameter ρ^0 indicates the correlation when $D_{ij} = 0$.

A square problem space of 10000 ha was then defined, and the unit distance within the problem space was set to 100 m, which is the linear measure of one side of a square territory 1 ha in size (so the problem space is 100×100 units and one area unit (1 ha) is one animal territory). We set a confidence level for Eq. 6 of 80%, and assumed that patch populations had a coefficient of variation = 0.5. We assumed that only 2000 ha of habitat could feasibly be retained among four habitat patches. And, for simplicity, it was assumed that all patches are large enough to support at least one breeding pair, and all function as patches in terms of connectivity and covariance. Thus, in terms of the formulations previously presented, the following parameters were set:

$M = 4$
$a_i = 2$
$\delta = -0.84$
$\psi = 0.5$
$\bar{L} = 2000$
$\bar{X} = 100$
$\bar{Y} = 100$
$\bar{R} = 0.56419$
$\bar{Q} = 1$

And, we set $\rho^0 = \text{pr}^0 = 0.9$ so that adjacent patches of habitat are highly connected and highly correlated, but still distinguished as separate patches. For demonstration purposes, both β and τ were set at 50, and θ and τ were varied between values of 0.75, 0.85, and 0.95.

4.2. Results and discussion

All of the solutions presented were obtained on a 486 microcomputer using a version of the "generalized reduced gradient algorithm" for solving nonlinear programs (originally developed by Abadie, 1978) called GRG2 in GINO (Liebman et al., 1986). Tolerances were set such that feasibility is assured within 1×10^{-6}. Multiple starts were employed in an effort to ensure global optimality, and all solutions presented appear to be global optima, but only local optima can be absolutely assured (Luenberger, 1973).

We initially solved the circular patch model with no size penalty ($\gamma = 0$, $b = 0$). Fig. 1a presents the solution with parameters set to reflect a species whose dispersal is not strongly inhibited by the inter-patch environment (i.e., $\theta = 0.95$, therefore pr_{ij} decays slowly with inter-patch distance) and where the disturbance agents tend to be rather local (i.e., $\omega = 0.75$, resulting in spatial correlations that decrease rapidly with distance). Two patches of habitat are clustered together, with the other two spread out about as far as possible. Note in Table 1 that the pairwise and joint probabilities of connectivity are still quite high – throughout the analysis, the solutions do not disperse habitat to the point that connectivity is severely sacrificed. At the same time, when an animal is capable of migrating across nontrivial distances, there is clearly an advantage in dispersing the habitat to some degree to reduce total

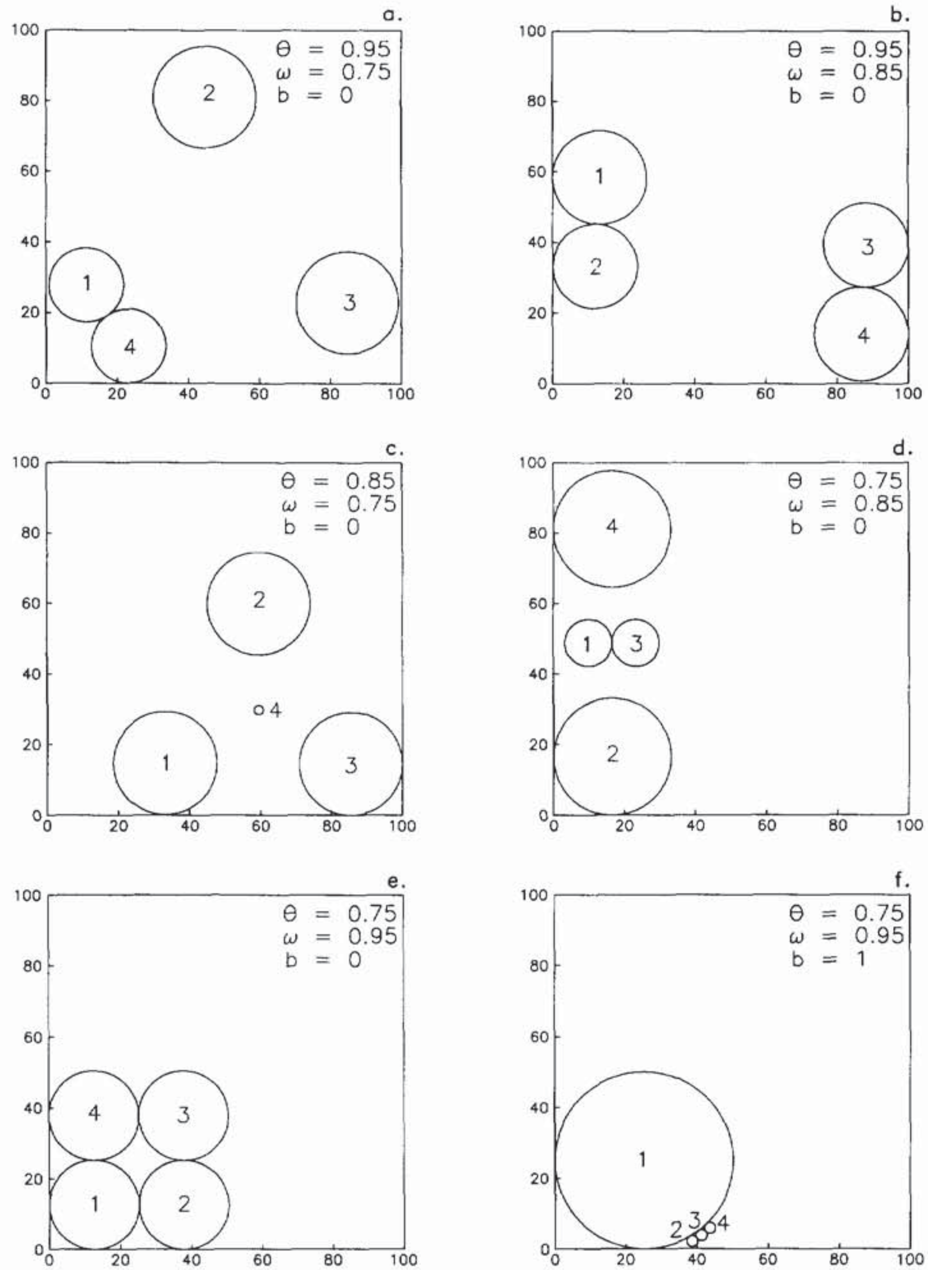

Fig. 1. Solutions of the circular patch formulation with varying levels of θ and ω. (a)–(e) have no size penalty whereas (f) implements an edge buffer of unsuitable habitat that penalizes patch size.

population variance. And, given the particular formulations developed, there are often ways to disperse the habitat and reduce total population variance without serious adverse effects on overall connectivity. The correlations between all patches except one and four are quite low (Table 1).

If ω is increased to 0.85, implying that spatial correlations do not decrease quite as rapidly with distance, then patches cluster into two pairs (Fig. 1b), which increases the connectivity relative to Fig. 1a, but still disperses the pairs widely. In Table 1, comparing the first with the second solution, $\omega = 0.85$ causes the solution population to decrease and the population standard deviation to increase.

In Fig. 1c, ω is returned to 0.75, and the θ is decreased to 0.85, indicating an inter-patch matrix that is more resistant to successful dispersal. This results in the patches being arranged in an equilateral triangle, with a "stepping stone" patch in the middle. In this type of solution, the assumption that any patch with $r_i \geq \bar{R}$ is fully functional in terms of connectivity (and correlation) is critical. In Table 1, this solution has some pairwise connectivity probabilities that are much lower than in previous solutions, but the joint connectivity probabilities are still quite high because of the location of patch four. For this connectivity, the solution endures much higher correlations between patch four and the other patches. It is still possible to keep the covariance relatively small, however, because the $\omega = 0.75$ (Table 1).

In Fig. 1d, the θ is decreased to 0.75 and the ω increased (again) to 0.85. These parameters reflect a very harsh inter-patch environment and disturbance factors that affect a large enough area to cause spatial correlations to decline only moderately with distance. The solution spreads patches two and four rather widely, but places patches one and three in between for connectivity. The solution endures high correlations between all patch pairs except two and four, resulting in a relatively high population standard deviation (Table 1). Looking across solutions in Table 1, it is clear that population levels with 80% confidence generally decrease with lower migration capabilities (caused by a harsh inter-patch matrix) and large disturbance factors.

Table 1
Connectivity probabilities, correlations, and objective function components for Fig. 1a–f

	Fig. 1a	Fig. 1b	Fig. 1c	Fig. 1d	Fig. 1e	Fig. 1f
pr_{12}	0.8996	0.9000	0.6170	0.8596	0.9000	0.9000
pr_{13}	0.8876	0.8752	0.6172	0.9000	0.8288	0.9000
pr_{14}	0.9000	0.8222	0.8946	0.8596	0.9000	0.9000
pr_{23}	0.8983	0.8729	0.6171	0.8596	0.9000	0.9000
pr_{24}	0.8875	0.8752	0.8946	0.0052	0.8287	0.9000
pr_{34}	0.8996	0.9000	0.8946	0.8596	0.9000	0.9000
PR_1	0.9989	0.9978	0.9845	0.9980	0.9983	0.9990
PR_2	0.9988	0.9984	0.9845	0.9804	0.9983	0.9990
PR_3	0.9988	0.9984	0.9845	0.9980	0.9983	0.9990
PR_4	0.9989	0.9978	0.9988	0.9804	0.9983	0.9990
ρ_{12}	0.00083	0.9000	0.0544	0.9000	0.9000	0.9000
ρ_{13}	0.00004	0.0095	0.0545	0.9000	0.9000	0.9000
ρ_{14}	0.90000	0.0029	0.5016	0.9000	0.9000	0.9000
ρ_{23}	0.00027	0.0088	0.0545	0.9000	0.9000	0.9000
ρ_{24}	0.00004	0.0095	0.5012	0.2334	0.9000	0.9000
ρ_{34}	0.00082	0.9000	0.5012	0.9000	0.9000	0.9000
objective function:						
B	3034.6	2831.8	2931.7	2557.7	2380.1	2115.7
$E(P)$	3995.4	3992.3	3938.3	3931.4	3993.1	3647.3
$V(P)^{0.5}$	1143.8	1381.5	1198.4	1635.4	1920.2	1823.3

In Fig. 1e, the θ is kept at 0.75 and the ω is increased to 0.95. These parameters again reflect an animal that is less capable of crossing nonhabitat area, but now with disturbance factors that are large enough to cause spatial correlations to decrease slowly with increasing distance. This implies that retaining connectivity will require close distances, and that dispersing habitat patches

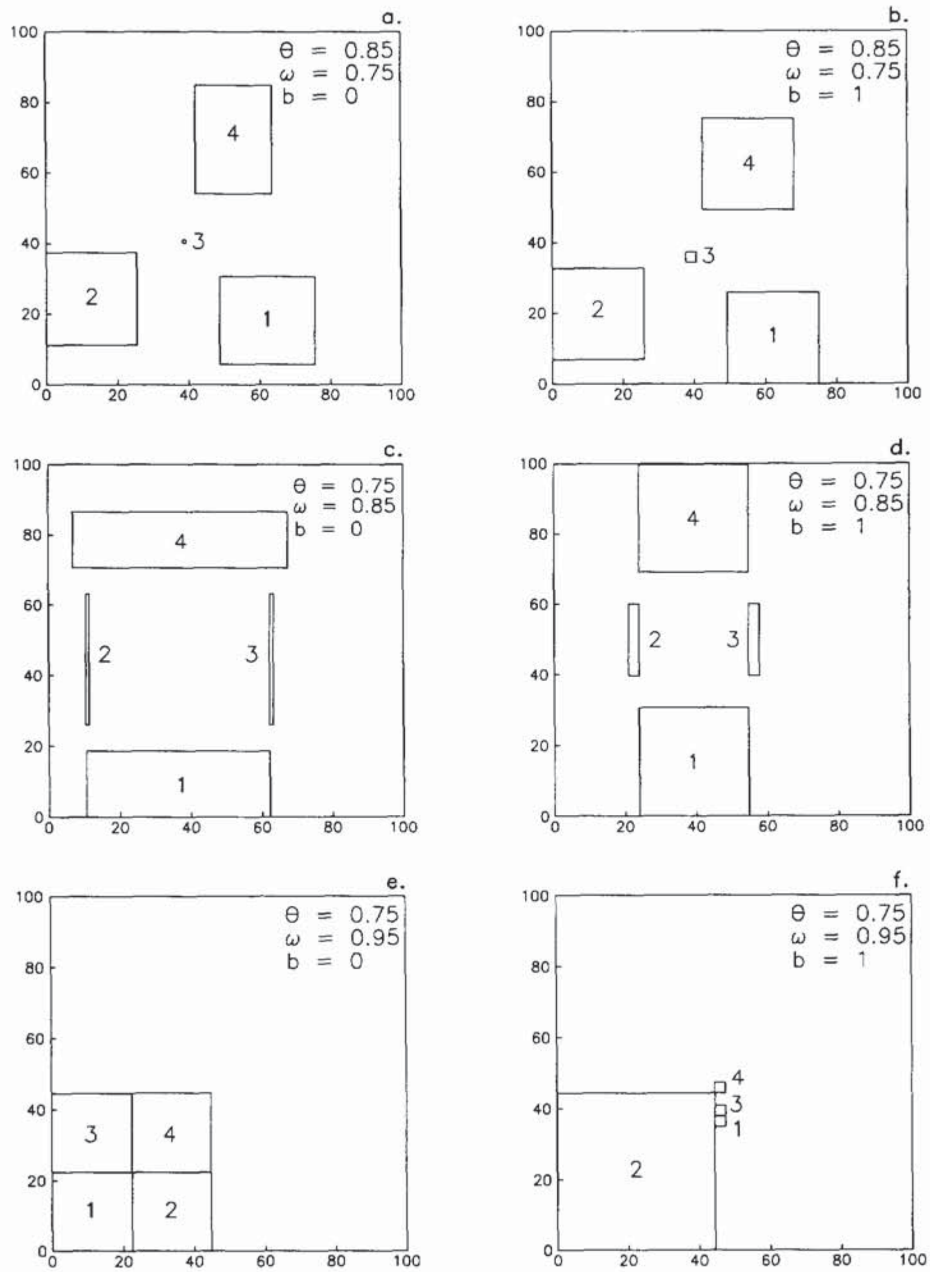

Fig. 2. Solutions of the rectangular patch formulation with varying levels of θ and ω. (a), (c), and (e) have no size or shape penalty, whereas (b), (d), and (f) implement an edge buffer of unsuitable habitat that penalizes patch size and shape.

gains relatively little in reducing population variances. The resulting solution is not surprising – four equal-sized patches are grouped as close together as possible. We did confirm that it is still optimal to retain these four patches as opposed to one large patch, because some variance reduction is still obtained (because $\rho^0 = 0.9$) and the joint connectivity probabilities are all very near 100% (Table 1).

This is not the case if a buffer 100 m wide ($\gamma = 1$, $b = 1$) is removed from the calculated usable habitat in each patch in Eq. 6 (Fig. 1f). Note that $\bar{R}$ was increased to 1.56419 to retain a minimum usable habitat for one species pair in each patch. Here, θ and ω are left at 0.75 and 0.95, respectively, but eliminating the buffer from usable habitat sufficiently penalizes small patches to result in one large patch and three minimum-sized patches placed adjacent to the large one. The buffer is about 15% of the habitat area in Fig. 1e, but is about 10% in Fig. 1f, which is enough to alter the optimal layout as observed. This demonstrates the difference that one might expect between edge-neutral species (Fig. 1e) and habitat-interior specialists (Fig. 1f) that cannot survive close to the edge (see Margules et al., 1994). Because circles are invariant with regard to shape, this buffer effect only penalizes size. Fig. 2a–f and Table 2 demonstrate the rectangular-patch formulation, which allows some variation in shape.

Fig. 2a presents the solution to the rectangular-patch formulation with $\theta = 0.85$ and $\omega = 0.75$ (as in Fig. 1c) and without the edge buffer penalty. The results are very similar to those in Fig. 1c, but with patch shapes that are somewhat more elongated. The equivalent solution with the buffer ($\gamma = 1$, $b = 1$) removed from usable habitat in Eq. 6 results in equalizing the three larger patch areas, increasing the interior patch size to meet the new constraint, and re-shaping the larger patches into squares (Fig. 2b). Note that $\bar{Q}$ was increased to 3.0 to retain a minimum usable habitat for one species pair in each patch. In Table 2, the effect of removing the edge buffer is to scale back the objective function (B) and its components $E(P)$ and $V(P)^{0.5}$, but to leave the connectivity probabilities and correlations almost unchanged.

The solution to the rectangular-patch formula-

Table 2
Connectivity probabilities, correlations, and objective function components for Fig. 2a–f

	Fig. 2a	Fig. 2b	Fig. 2c	Fig. 2d	Fig. 2e	Fig. 2f
pr_{12}	0.6117	0.6045	0.8985	0.8821	0.9000	0.9000
pr_{13}	0.8980	0.8995	0.8985	0.8821	0.9000	0.9000
pr_{14}	0.6117	0.6045	0.000015	0.0007	0.9000	0.8997
pr_{23}	0.8982	0.8996	0.00002	0.0066	0.9000	0.9000
pr_{24}	0.6046	0.6028	0.8985	0.8821	0.9000	0.9000
pr_{34}	0.8982	0.8996	0.8985	0.8821	0.9000	0.9000
PR_1	0.9846	0.9843	0.9897	0.9861	0.9990	0.9990
PR_2	0.9844	0.9842	0.9897	0.9862	0.9990	0.9990
PR_3	0.9989	0.9990	0.9897	0.9862	0.9990	0.9990
PR_4	0.9844	0.9842	0.9897	0.9861	0.9990	0.9990
ρ_{12}	0.0530	0.0510	0.9000	0.9000	0.9000	0.9000
ρ_{13}	0.5995	0.7097	0.9000	0.9000	0.9000	0.9000
ρ_{14}	0.0530	0.0510	0.0098	0.0825	0.9000	0.9000
ρ_{23}	0.6104	0.7176	0.0116	0.2613	0.9000	0.9000
ρ_{24}	0.0510	0.0506	0.9000	0.9000	0.9000	0.9000
ρ_{34}	0.6104	0.7176	0.9000	0.9000	0.9000	0.9000
objective function:						
B	2933.9	2486.7	2744.7	2270.7	2381.8	2088.9
$E(P)$	3937.9	3336.3	3958.8	3307.2	3996.0	3601.0
$V(P)^{0.5}$	1195.1	1011.5	1445.3	1233.9	1921.6	1800.2

tion with $\theta = 0.75$ and $\omega = 0.85$ (as in Fig. 1d) and no buffer penalty makes considerable use of the shape flexibility in the rectangular-patch model, increasing the objective function by about 7% (Fig. 2c, Table 2). Two long, narrow patches are used to "connect" two larger patches while at the same time keeping the distance between the larger patches quite large (and correlation quite small, see Table 2). The assumption on $\overline{Q}$ is again critical, because the model implicitly assumes that patches two and three are wide enough to serve as corridors connecting patches one and four. Incidentally, patches two and three are also connected by patches one and four, and patches one and four are apparently elongated to reduce the correlation between two and three. An equivalent solution with the adjustments to remove the buffer from usable habitat squares-up patches one and four and widens patches two and three to meet the new $\overline{Q}$ level (Fig. 2d). Because of the problem space limits and the geometry of patches one and four, this also implies shortening patches two and three, and shortening the distances between most of the patches. The solution values are quite different for the parameterizations depicted in Fig. 2c and d (Table 2).

The solution to the rectangular-patch formulation with $\theta = 0.75$, $\omega = 0.95$ and no buffer penalty is similar to the circular-patch formulation. In fact, the advantages of compaction cause the optimal solution to create near-square shapes even without the buffer penalty (cf. Fig. 2e and Fig. 1e). When the buffer is removed from the usable habitat (Fig. 2f), however, a solution much like Fig. 1f is obtained.

Whether a species will persist in a fragmented environment is a question that has typically been addressed through simulation of metapopulations (Kareiva, 1990). Under this spatial metapopulation approach, patch layout is essentially fixed and the impacts of that layout on the temporal dynamics of a species' population are documented (see for example Bowers and Harris, 1994). Metapopulation modelling offers an analysis approach that captures complex population dynamics when there is little opportunity for land managers to alter the configuration of remaining habitat patches. If the configuration of remaining habitat has not be specified, then spatial optimization offers an alternative analysis that permits prescribing a patch layout that "best" meets the requirements for long-term population survival. Although the circumstances of the conservation problem will likely dictate whether simulation or optimization is most appropriate, there is no inherent reason for these approaches to be mutually exclusive. Using spatial optimization to hypothesize a spatial layout which, in turn, is tested through simulation of metapopulation dynamics, would undoubtedly provide shared insights into the analysis of populations in spatially structured environments.

5. Conclusion

The case example is not intended as a realistic application of the model formulations. Any real-world situation would have many more constraints, and would probably involve many species and any number of other complicating factors. Rather, the purpose of the case example is to demonstrate the sorts of solutions that the models generate in a relatively simple, interpretable setting. Our objective was to mathematically capture the mutually inconsistent ecological concerns of habitat fragmentation and spatial correlation into a single model and show that the optimal balance between these concerns can, in principle, be determined through optimization procedures. The case example solutions do suggest an ecological principle that the best spatial arrangement for habitat will often include a "mixed strategy" that manages to connect the habitat but still spread it out at the same time (such as in Fig. 1d and Fig. 2c and d). Also, it is clear that simple "ecological principles" will be difficult to develop, because species with different life history attributes (represented here by dispersal capability) and environmental disturbance agents with different spatial magnitudes both imply radically different optimal layouts.

This paper is obviously an initial, developmental effort in a relatively new research area. Strong simplifying assumption were necessary, and much work clearly remains to be done. We hope, however, that this first attempt encourages optimization thinking and modelling efforts aimed at ecological problems involving trade-offs between competitive considerations.

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